

Observations on the foraging behaviour of *Myrmicaria brunnea subcarinata* (Smith) (Hymenoptera: Formicidae) in a tropical rainforest in Sarawak (Malaysia)

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Abstract. As a contribution to the knowledge of the natural history of *Myrmicaria brunnea subcarinata* (Smith, 1857), we studied the territory, circadian activity patterns, diet composition, trophobiotic interactions and fighting success of a colony of this species in an alluvial forest in Gunung Mulu National Park (Borneo, Malaysia). The territory size of the focal colony, which comprised 6,000 to 8,000 individuals living within a single nest, was approximately 270 m². Many permanent foraging trails were subterranean and total observed trail length was about 44 m. Ants were active at the nest throughout the 24-hour cycle, with increased foraging activity during the night. The food spectrum of the species included mostly animal prey, but also herb particles and plant juice. Additionally, *M. brunnea subcarinata* was found in trophobioses with several bugs (Coreinae) and other hemipteran species at stems of the climbing bamboo *Dinochloa trichogona* and other plant species. Observations at baits showed that the species defended resources successfully in about 2/3 of all experimental interactions, with *Pheidologeton affinis* being its most effective competitor.

Keywords: Borneo, competition, foraging activity, Myrmicinae, territoriality, trail system, trophobiosis, tropical rainforest

INTRODUCTION

The genus *Myrmicaria* Saunders, 1842 (Formicidae: Myrmicinae) is found in the Afrotropical region (49 species and subspecies) and the Oriental region (18 species and subspecies) (Bolton *et al.* 2006) and includes two groups of morphologically and ecologically different species. The members of the *Myrmicaria brunnea* group, e.g. *M. carinata* (Smith, 1857) and *M. opaciventris* Emery, 1893, have subterranean nests, while *M. arachnoides* (Smith, 1857) and the other members of the *M. arachnoides* group are arboreal nesting species (Bakhtiar & Yamane 2006). The foraging sites of the species differ strongly: in Africa most species forage on the ground surface, but *M. salambo* Wheeler, 1922 is an

arboreal forager (Weißflog 2001). Species of the *M. arachnoides*-group are arboreal nesters but also forage on the ground (Bakhtiar & Yamane 2006). The best-studied species up to now is the African *M. opaciventris* that inhabits polydomous, polygynous colonies with approximately 7,000 – 20,000 individuals in each nest (Kenne & Dejean 1999).

In Sarawak (Malaysia), the taxon *Myrmicaria brunnea subcarinata* (Smith, 1857) lives in primary forests, often in alluvial sites. While subspecies are not generally recognised in myrmecology and this is suspected to be a distinct species, the subspecific name is retained here pending taxonomic revision. Compared to *M. brunnea brunnea* that is found in India, *M. b. subcarinata* is slighter, more slender and lighter in colour, it is

known from Burma and extends to Borneo (Bingham 1903). Though it is apparently not uncommon, details about its life history are still unavailable. The aim of this study was to obtain basic-level information about foraging behaviour and activity of this species.

MATERIAL AND METHODS

Study area and time of the study

The study took place in Gunung Mulu National Park (GMNP) in Sarawak, Malaysia, situated on the island of Borneo near the southern border of Brunei (04°02' N 114° 48' E). GMNP encompasses an area of 520 km² and includes Sarawak's second highest mountain (Gunung Mulu, 2,377 m), with a geological foundation of limestone, sandstone and alluvial clays. The three main forest types in that area are alluvial forest, limestone forest and dipterocarp forest (Hazebroek & Morshidi 2001, Web Ref 1). Yearly rainfall ranges from 4,000 to 5,000 mm, with slightly higher values in April-May and October-November (Web Ref 2). The study was conducted from 12 September to 13 October 2006 with a few additional data collected from 8 August to 14 September 2007. Our study plot was located in an alluvial forest that was observed to be flooded several times a year by the nearby river; however, as the area with the nest was slightly elevated, it was probably flooded only rarely. To the east, the plot was bordered by a gap caused by a large fallen tree. Undergrowth varied from very light to dense vegetation that mainly consisted of scrubs and lianas. The leaf litter layer at the nest site was estimated to be about 2-3 cm thick.

Weather conditions during our study were unsteady, with mostly dry mornings, but frequent heavy rainfalls and strong winds from noon until evening. An especially heavy rain flooded large parts of the lower regions of the study area for several days.

Spatial distribution

We used tuna baits to study the spatial distribution of ants (tuna fish was placed on pieces of newspaper such that the paper was soon soaked with tuna oil, keeping the bait attractive even after

all of the fish had been consumed). Initially, we placed 12 baits in a grid and followed the trails of the ants from the baits back to their nests. Additional baits were placed to study the spatial distribution of these ant colonies. We followed returning foragers to their nest to obtain the foraging range of the species. Altogether we placed 60 baits altogether in the study plot, covering an area of approximately 800 m². Using a compass and measuring tape, we mapped the relative positions of all baits and trails of the ants, compensating for measuring errors by multiple measurements from several positions. Measurements were accurate to 2° and 10 cm.

We took samples of all ant species at the baits. Baits were checked continuously at intervals of approximately 10-15 minutes until either a) the bait was completely exploited by a species or a combination of species, or b) a species or a combination of species obviously dominated it. This included cases where two hostile species managed to exploit the same bait in each other's presence. Each day on which a species was found at a bait was counted as "one encounter" for that species. A bait was considered "used" by each species that a) had exploited the bait or b) was still present at the last daily observation, assuming there was still food left. We counted conflicts by the number of opposed species; that is, a conflict of three species at the same bait was counted as two hostile encounters for each of the species. Species that were able to "use" a bait in the presence of an other species were considered as "winners".

Observations

We used two *Myrmicaria brunnea subcarinata* colonies in the study plot as focal colonies. On the first colony we conducted observations of foraging activity, food intake, ground speed of foragers and trail structure, and the second one was used only for observations of foraging activity.

We followed newly detected *M. brunnea subcarinata* trails whenever possible and classified them as either permanent ('soil trails') or temporary. We measured and mapped all soil trails as well as selected temporary trails and noted the ground types.

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For comparison of forager speed, we timed worker ants running on two different substrate types, soil and bare roots, both of which were frequently used as paths by ants. On each substrate type 20 workers were timed for a distance of 20 cm. We calculated running speed for each group in cm/s.

We counted ant traffic at a specific location on the main trail near the nest entrance of the focal colony for a duration of 10 minutes per observation period of one hour, using two mechanical handheld counters (inbound and outbound, respectively). Ant activity was later re-calculated as the number of individuals per minute.

We conducted a 24h-observation at the first focal colony from 1 October at 08:00 h until 2 October at 07:10 h. Hourly observations included ant activity and food intake. Additional observations of food input at the nest were added. A similar round-the-clock activity observation was performed from 13 September at 16:00 h until 14 September at 15:10 h at the second focal nest in the same area.

To investigate food types, we observed inbound ants at the main nest entrance. Every ant encountered carrying a load was picked up, the load being stored in alcohol and the ant set back on the trail. This was done for 30 periods of 10 minutes at various times of the day. Food samples were assigned numbers and taken back to the laboratory for identification with a microscope. The number of loaded ants collected in 10 minutes was compared to the total number of counted ants in the same period to calculate the percentage of ants carrying load.

We noted and sampled several trophobioses (comprising plant, trophobionts and ants) that included *M. brunnea subcarinata* as a partner and were found in the vicinity of the focal nest. Identification of samples of ants and trophobionts was conducted in the laboratory.

Analysis

The statistical analysis was performed using JMP 5.1.2 (SAS Institute) software.

RESULTS

Focal colony

The first focal *M. brunnea subcarinata* nest was situated under a dead yet upright tree, and had one main and one secondary entrance. Based on the nest diameter of 45-50 cm, we estimated the colony size to be approximately 7,000 – 9,000 individuals (Kenne & Dejean 1999).

We found the species to construct tunnel-like mud-shelters on the bark of trees up to 1.50 m from the ground. In three cases we found bugs (Heteroptera: Coreinae) beneath the mud layer, but neither larvae nor eggs of the Coreinae. During several observations we discovered only a few worker ants (1-5) in these shelters. We did not observe true polydomy.

Trail system

The trail system of *M. brunnea subcarinata* consisted of two main components: ‘soil trails’ and ‘temporary trails’. The soil trails, which functioned as ‘main roads’, often included sections that ran under the leaf litter layer and were cut into the ground, forming grooves sheltered by a layer of leaves. These sections were held clear of obstructions like small sticks and stones. The temporary trails diverged from the trunk trails and served as aboveground foraging trails to nearby food sources. Apart from the trails on the ground, *M. brunnea subcarinata* was also found on low shrubs and similar small plants; the ants used them for foraging and for accessing their trophobionts (see below).

The longest among the measured trails exceeded 18 m in length: in fact we found individuals of the focal colony on temporary trails more than 21 m away from their nest (Fig. 1). Using the outermost bait positions where *M. brunnea subcarinata* was still found, we estimated the territory size to be approximately 270 m² (Fig. 1). Total length of observed trails in this territory was 43.75 m.

Foraging speed of foragers differed significantly between the two chosen ground types (Wilcoxon / Kruskal-Wallis test: $n_{1,2} = 20$; $Z = -5.31559$, $P < 0.0001$); ants ran slower on soil trails

(mean = 3.18 cm/s; SE = 0.14; range = 2.01 – 4.81 cm/s) than on roots (mean = 7.52 cm/s SE = 0.4; range = 3.96 – 10.2 cm/s).

Diet

Food intake of *M. brunnea subcarinata* included insects (ants, cicadas, termites, butterflies and larvae), spiders, snails, earthworms, plant particles and amphibian larvae (probably tadpoles of *Microhyla* sp. (Microhylidae)) (Fig. 2). In one case a gecko carcass was used as a food source. Often large prey was torn into pieces prior to transport by worker ants instead of being carried whole. Furthermore, we observed ants collecting parts of fruits from the ground. We found other food of vegetable origin, which however could not be identified; sometimes the ants carried also small pieces of fungus. *M. brunnea subcarinata* ants

were also found sucking plant juice on *Melastoma* stems and using honeydew from trophobiotic interactions (see below), but attempts to use sugared water as a bait failed. Tuna baits, however, were readily accepted. At the nest entrance of the focal colony mean percentage of ants (inbound only) that were loaded was 6.27 ± 0.71 % (mean \pm SE; range 0 – 13.85 %, $n = 495$ checked ants).

Trophobiotic interactions

On multiple occasions, we observed trophobioses with various stages of bugs (Heteroptera: Coreinae) and cicadas (Cicadina: Delphacidae and Membracidae) mostly on the climbing bamboo *Dinochloa trichogona* or *Macaranga*, but also on other plants (Table 1). Sometimes we found single bugs that seemed to be trophobionts in the mud shelters at tree stems. The number of ants in

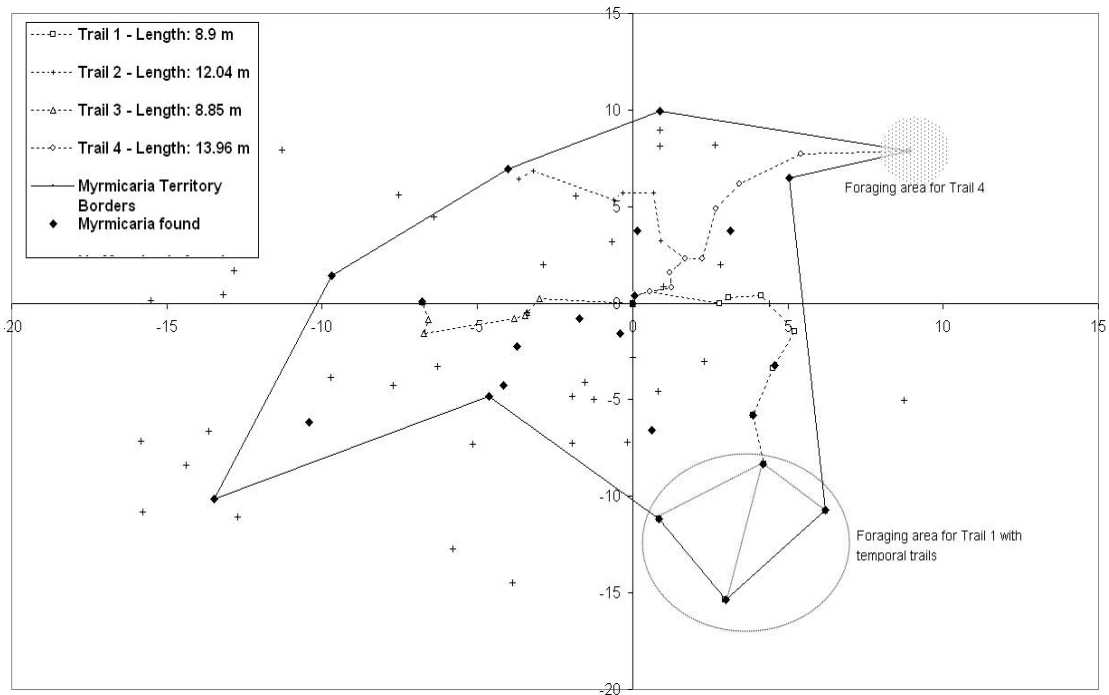


Fig. 1. *Myrmicaria* trail system and estimated territory borders. The nest entrance of the focal colony is at (0,0). Distances are in metres, north is up. “+” indicates the position of baits. The area was estimated at 270 m². Trails 1 and 4 shared a common section at the beginning and were permanently used at varying frequencies. Trails 2 and 3 were temporary, as were the most distant sections of trails 1 and 4. The western part of the explored area was cut off to allow the use of a smaller enlargement scale for improved readability.

these trophobiotic interactions varied greatly, ranging from less than a dozen to more than 80 individuals (see Table 1). We also observed workers of *M. brunnea subcarinata* sampling honeydew at tree sucking scale insects.

Activity patterns

Workers of *M. brunnea subcarinata* were active at any given time of day or night (Fig. 3). When we divided the span of our 24-h observation into day

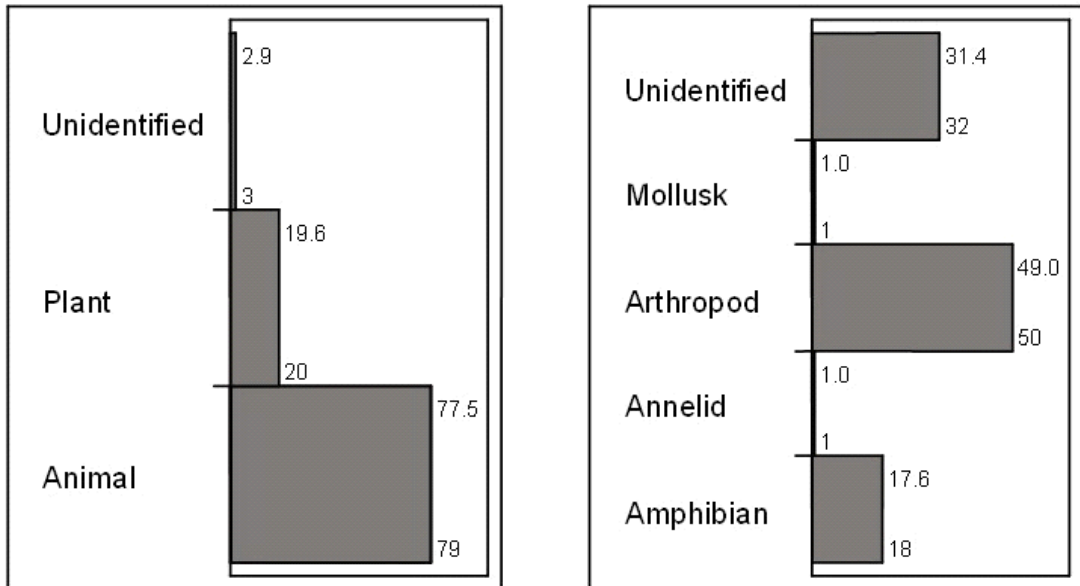


Fig. 2. Diet diagram of *Myrmecaria* ($n = 102$). Given are the absolute numbers (lower number) and the respective percentage (upper number) of loads with which foragers returned to the nest.

Table 1. Hemipterans that interacted with *M. brunnea subcarinata* and details on the position of the trophobioses and the numbers of interacting animals.

Type of trophobiont	Type of plant	Position of trophobiosis	n	# of ants per position \pm SD	# of trophobionts per position \pm SD	Ant / hemipteran ratio \pm SD
Auchenorrhyncha: Delphacidae	<i>Dinochloa trichogona</i>	Stem / leaf base	4	8 \pm 6.98	8.5 \pm 9.95	1.13 \pm 0.51
Heteroptera: Coreinae	<i>Dinochloa trichogona</i>	Stem / leaf base *	8	11.43 \pm 8.10	6 \pm 6.08	2.76 \pm 2.88
Sternorrhyncha: Psylloidea	small tree	Trunk	1	82	78	1.05
Auchenorrhyncha: Cicadellidae	small shrubs	Branch *	4	12 \pm 8.76	2.25 \pm 1.50	6.15 \pm 2.79
Auchenorrhyncha: Membracidae	small shrubs	stem / leaf	2	11.5 \pm 4.95	5 \pm 4.24	2.94 \pm 1.50
Heteroptera: Coreinae	large tree	Bark *	1	70	40	1.75
Sternorrhyncha: Coccoidea	large tree	Bark	1	25	115	0.22

* soil shelter

(7:00–18:00 h) and night (19:00–6:00 h), ant activity was significantly higher at night time (24.11 ± 1.36 ants per minute for first colony, 22.63 ± 2.88 ants per minute for second colony) than during the day (15.36 ± 0.97 ants per minute for first colony, 9.72 ± 0.6 ants per minute for second colony) (one-tailed *t*-test; first colony: $n_{\text{day}} = 19, n_{\text{night}} = 12; t = -5.39, P < 0.001$; second colony: $n_{\text{day}} = 12, n_{\text{night}} = 12; t = -4.39, P < 0.0001$), while the percentage of inbound ants loaded with food was significantly larger during daytime ($8.2 \pm 0.85\%$) than at night ($3.21 \pm 0.53\%$) (one-tailed *t*-test; $n_{\text{day}} = 19, n_{\text{night}} = 12; t = 4.31, P < 0.001$) (Figs. 4 and 5).

Competition

As was expected, we found many other ant species within the foraging range of *M. brunnea subcarinata*. These competing species showed

various behaviours in terms of aggression and dominance. The five most frequently encountered competing species were *Pheidologeton affinis* (Jerdon, 1851), *Crematogaster modiglianii* (Emery, 1900), *Camponotus rufifemur* (Emery, 1900), *Lophomyrmex bedoti* (Emery, 1893) and *Tetramorium* sp. (near *vertigum*).

In our baiting experiments we encountered *M. brunnea subcarinata* 31 times at the baits. In 18 of these 31 encounters, *Myrmicaria brunnea subcarinata* met at least one other species on the bait. In total, this led to 23 conflicts, 10 (43%) of which were won (Table 2), allowing *Myrmicaria brunnea subcarinata* to exploit 9 of 18 (50%) baits against hostile resistance.

The most challenging opponent turned out to be *P. affinis*, which held the bait even in the presence of *M. brunnea subcarinata* in five out of five cases (Table 2). *Myrmicaria brunnea*

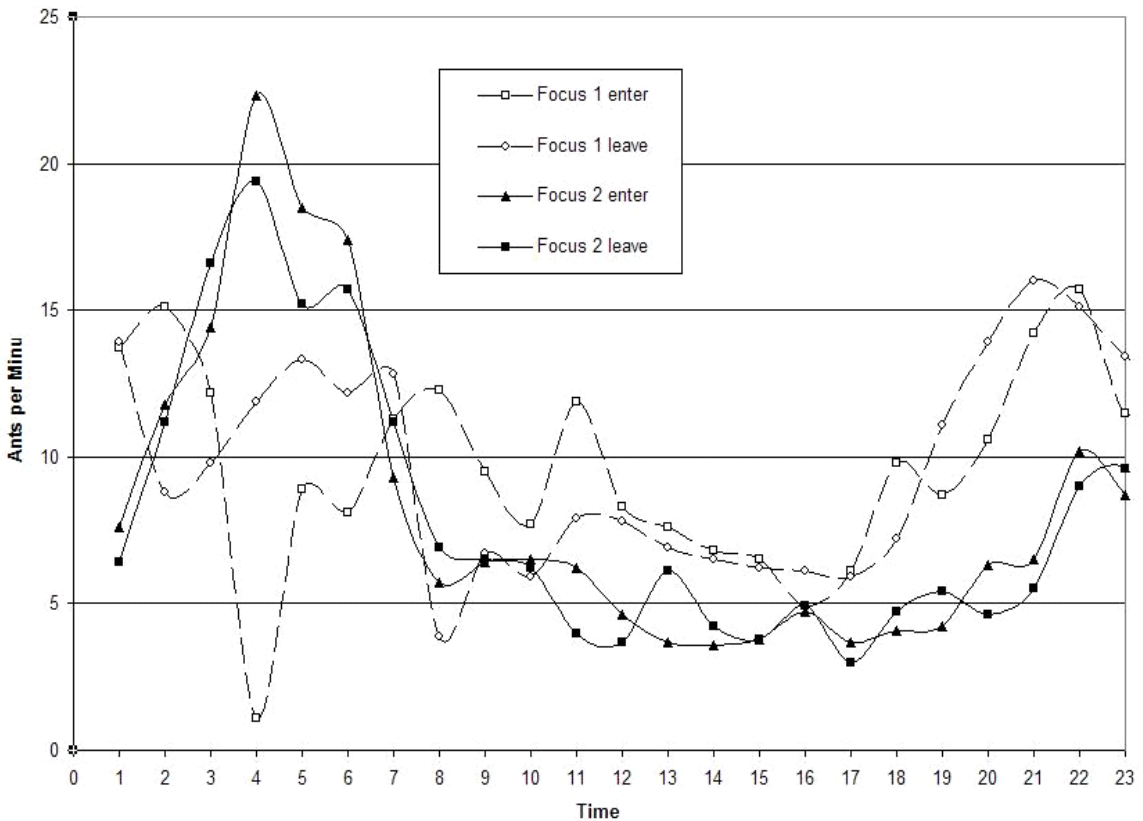


Fig. 3. Activity patterns at two focal colonies' entrances of *M. brunnea subcarinata* by time of day.

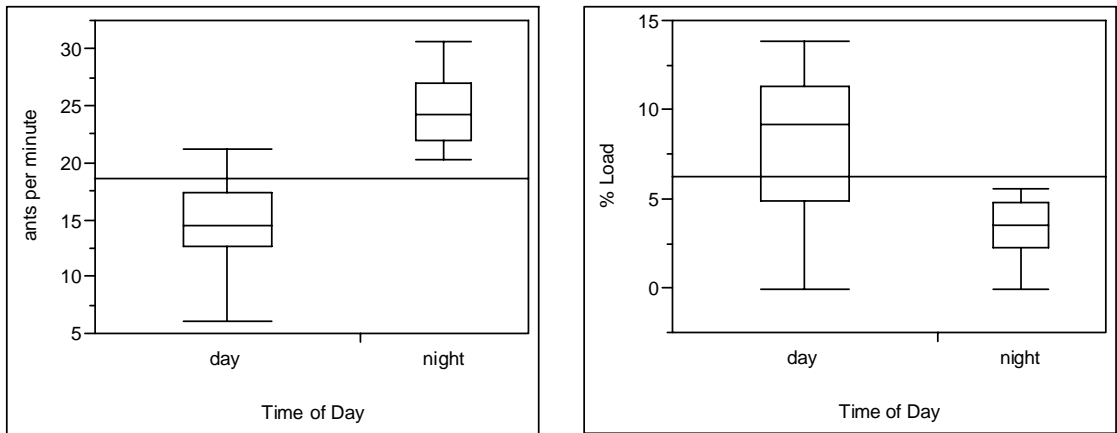


Fig. 4. Total traffic (left) and load percentage (right) at the *M. brunnea subcarinata* focal colony main entrance by day (7:00 – 18:00 h) / night. (19:00 – 6:00 h). Horizontal Line: Overall mean.

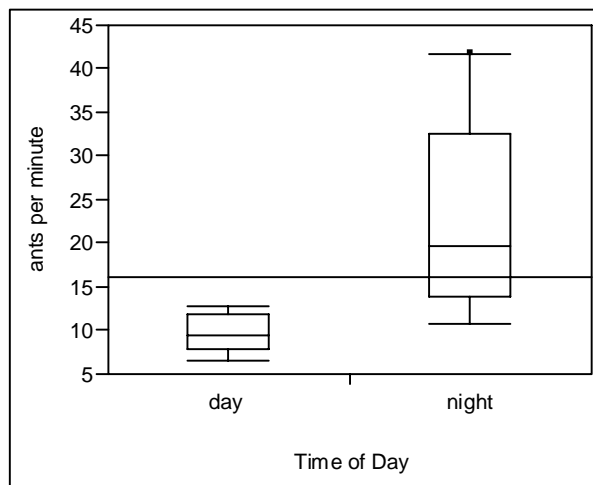


Fig. 5. Total traffic at the second *M. brunnea subcarinata* colony by day (7:00 – 18:00 h) / night (19:00 – 6:00 h). Horizontal Line: Overall mean.

subcarinata had to retreat in four out of those five cases, while in the remaining observation both species utilised the bait together. The workers of *P. affinis* were distributed all over the study area. They built vast networks of mud-roofed tunnels on open ground and within the leaf litter layer. A nest was found in close proximity (3.25 m) to the focal colony. At the baits they appeared in large numbers. Like *L. bedoti* (see below), they monopolised baits quickly and vigorously defended them against any competitor in overwhelming numbers.

Lophomyrmex bedoti was among the species most numerously encountered together with *M. brunnea subcarinata* and an effective opponent, exploiting the baits in three out of five (60 %) cases in direct confrontation (Table 2); one of these confrontations was not only against *M. brunnea subcarinata*, but also against *Pheidole* sp. and *Paratrechina* sp. at the same time. *Lophomyrmex bedoti* workers tended to occupy and monopolise baits only a few minutes after their placement, showing aggression against any other ant species. Surprisingly, we also found them in close proximity to the nest of *M. brunnea subcarinata*. The two species frequently shared or crossed trails without apparent aggression, in spite of *L. bedoti* having a nest close by. In this location, the *M. brunnea subcarinata* trail was a prominent soil trail close to the focal colony nest entry, whereas the *L. bedoti* trail was a temporary one.

Workers of *Tetramorium* sp. (near *vertigum*) were the weakest opponents of *M. brunnea subcarinata*; they withdrew in 5 out of 6 encounters. There was a nest of this species 1.3 m away from the focal colony.

In 16 experiments we were able to identify the first arrivers at a bait with certainty. Out of these 16 cases, *M. brunnea subcarinata* arrived first in four (25 %) cases. *Tetramorium* sp., *Cr. modiglianii* and *L. bedoti* were the first to arrive in three cases each.

In four out of 18 cases when *Cr. modiglianii* or *C. rufifemur* were encountered, these parabioc species collaborated in exploiting the baits. Typically *Cr. modiglianii* appeared first, while *C. rufifemur* followed some minutes later to carry the tuna away to the nest shared by the two species. We found two parabioc nests in the survey plot at distances of 7.21 and 8.21 m away from the focal colony.

M. brunnea subcarinata encountered the *Cr. modiglianii* alone only one time although their nests existed close together; there were monospecific *Cr. modiglianii* nests at distances of 2.8 and 0.4 m. In that encounter, the *M. brunnea subcarinata* scouts were already vastly outnumbered by *Cr. modiglianii* and retreated without apparent offensive activity. An apparently monospecific nest of *C. rufifemur* was found 8.61 m away from the nest of *M. brunnea subcarinata*.

Additional species of other genera that we observed at the baits included *Acanthomyrmex ferox* Emery, 1893, *Philidris* sp., *Oecophylla smaragdina* (Fabricius, 1775), *Recurvidris browni* Bolton, 1992 and *Paratrechina* sp. (Tables 2, 3). We also found several *Pheidole* spp. and occasionally *Aenictus* sp. swarmed in the area.

DISCUSSION

It is difficult to draw definite conclusions from the available data, as we observed only two nests of *M. brunnea subcarinata* during our one-month study. We have shown that the species has a very broad food spectrum, including herb pieces, plant juice, honeydew and several kinds of food of animal origin. *M. brunnea subcarinata* is apparently a food opportunist, capable of flexible reactions to sudden changes in food supply. A good example of the opportunistic foraging pattern was the amphibian larvae that were sampled by *M. brunnea subcarinata* workers a few days after strong rain and which certainly are not a common prey of the species. The results of an analysis of the stable nitrogen isotope ratios of this ant species underline its opportunistic lifestyle. *Myrmicaria brunnea subcarinata* sampled from Gunung Mulu National Park had a medium delta value of 4.87‰ ^{15}N ($n = 5$; $\text{SD} \pm 0.26$), indicating that this species is on the second trophic level of the respective food web, in a similar trophic position to species of *Lophomyrmex* and *Pheidole* (Mezger & Pfeiffer, unpublished data; for method see Blüthgen *et al.* 2003). ^{15}N signatures collected by Davidson *et al.* (2003) in a rainforest in Brunei were at 2.5‰ ^{15}N ($n = 4$) for a trophobiont-tending species of the *M. brunnea* group, indicating a less carnivorous diet; however, as the two studies have not been calibrated together, this difference could also be due to different ^{15}N levels of the surroundings.

Table 2. Conflict Matrix. Each number represents the number of times the species in the matching row did exploit a bait in presence of the species in the matching column. Empty fields mean there were no encounters between the two species. The two rightmost columns show the total number of hostile encounters (“Total”) and the cumulative number of opponents against which a bait (or a part of it) was held (“Won”). Encounters with more than one opponent at a time count as multiple encounters. A “0” in the field of two opposing species means that both were driven away by a third opponent (e.g. *Pheidole* vs. *Paratrechina*) in the same encounter.

Species	Pg	Ca	Gn	Cr	Pd	Lo	Ac	Ph	Mbs	Te	Myp	Re	Pa	Won	Total	Percentage
<i>Pheidologeton affinis</i> (Pg)				1					5	1				7	7	100.0
<i>Camponotus ruffemur</i> (Ca)					1							1		2	2	100.0
<i>Gnamptogenys</i> sp. (cf. <i>Gabata</i>) (Gn)				2										2	2	100.0
<i>Crematogaster modiglianii</i> (Cr)	0			1	1				1			1		4	6	66.7
<i>Phildris</i> sp. (Pd)			0								2			2	3	66.7
<i>Lophomyrmex bedoti</i> (Lo)	0	2	0			1	1	1	3	1			1	9	14	64.3
<i>Acanthomyrmex ferox</i> (Ac)				1		1	0	1	1	1				3	5	60.0
<i>Pheidole</i> sp. (Ph)				0		1	1	1	1	1			0	3	6	50.0
<i>Myrmicaria brunnea subcarinata</i> (Mbs)	1		0	0	2	1	0	0	1	6			0	10	23	43.5
<i>Tetramorium</i> sp. (near <i>noratum</i>) (Te)	0				1	0	0	0	1					2	11	18.2
<i>Myrmicaria pseudoflava</i> (Myp)			0											0	2	0.0
<i>Recurvidris browni</i> (Re)		0	0											0	2	0.0
<i>Paratrechina</i> sp. (Pa)					0		0	0	0				0	0	3	0.0

The circadian activity pattern showed higher activity during night-time, but with a decreasing percentage of prey-loaded ants. However, when comparing the activity profiles of the two colonies, it is obvious that the day / night difference is more prominent in the second than in the first colony. Environmental factors may affect the circadian activity patterns, as well as the input of prey (see observations of Pfeiffer & Linsenmair (2000) on the foraging of the Bornean formicine *Camponotus gigas*).

Myrmicaria brunnea subcarinata showed a surprisingly long foraging distance, exploiting baits up to 20 m away, while in other cases ignoring baits in close vicinity to the nest. Soil trails resembled the tunnels described for *M. opaciventris* by Kenne & Dejean (1999) in their early excavation stages; the trenches were dug several centimetres into the earth and occasionally covered by leaves and soil.

In our observation area *M. brunnea subcarinata* was the species that was found at most of the baits. Moreover in 17 of 31 cases (= 55 %) it was the first or only species at the bait, thus showing their ability to rapidly discover and exploit a resource. This may be partly due to its elaborate trail system, but points also to effective recruitment mechanisms (Rastogi *et al.* 1997). The decision which bait to exploit might be influenced by the competitors normally found in that area. *Myrmicaria brunnea subcarinata* held the bait in 50 % of the encounters against a total of 10 competitors; in one of these encounters it defended the bait against *Tetramorium* sp. (near *vertigum*) and *Acanthomyrmex ferox* at the same time. Five victories were solely gained against *Tetramorium* sp., a species withstanding competitors in 2 out of 11 (18 %) conflicts. When *L. bedoti* (conflicts won: 9/14 = 64 %) or *Pheidologeton affinis* (conflicts won: 7/7 = 100 %) was involved, *M. brunnea subcarinata* tended to withdraw from the baits (Table 2). These figures suggest that the species' offensive capabilities were located in the middle range, between *P. affinis* and *Tetramorium* sp., but the high percentage (13 / 31 cases, 41 %) of monopolised baits in the absence of a competitor suggests more conflict-avoiding than aggressive behaviour. This exploitative competitive ability, if interpreted

Tetramorium sp., a species withstanding competitors in 2 out of 11 (18 %) conflicts. When *L. bedoti* (conflicts won: 9/14 = 64 %) or *Pheidologeton affinis* (conflicts won: 7/7 = 100 %) was involved, *M. brunnea subcarinata* tended to withdraw from the baits (Table 2). These figures suggest that the species' offensive capabilities were located in the middle range, between *P. affinis* and *Tetramorium* sp., but the high percentage (13 / 31 cases, 41 %) of monopolised baits in the absence of a competitor suggests more conflict-avoiding than aggressive behaviour. This exploitative competitive ability, if interpreted correctly, would mark them as submissives (Davidson 1998) or opportunists (Wilson 1971).

Other very strong competitors of *M. brunnea subcarinata* were *Camponotus ruffifemur* (conflicts won: 2 / 2 = 100 %) and *Crematogaster modiglianii* (conflicts won: 4 / 6 = 67 %). These two species never undertook any hostile actions against each other, they cooperated and exploited the same bait together and therefore none of their encounters were regarded as "conflicts" for means of counting. We found two nests in which both species nested together. Similar parabioses are mentioned in Kaufmann (2002) for species of the same genera found in arboreal ant gardens and in Davidson *et al.* (2007) between Bornean *Camponotus (Colobopsis)* species and several *Polyrhachis* species. The success of the mutualism between the *Ca. ruffifemur* and *Cr. modiglianii* was based not only on their ability to defend their resources, but also on their capacity to quickly monopolise bait before other species arrived. In eight of 14 times when we met at least one of these species at the baits no other species was present. This success both in exploitative and encounter competition was also mentioned by Davidson (1998) for the South American parabiotic species pair *Camponotus femoratus* (Fabricius) 1804 and *Crematogaster limata* Smith 1858 var. *parabiotica*. In that case Davidson (1998) assumed that interspecific territoriality by one or both of these arboreal species contributed to their exploitative ability. Although the Bornean species are also often arboreal nesters (D. Mezger, personal observations), in this specific case the nests were underground and we did not observe ants defending an absolute territory. Moreover,

absolute territories are unlikely for ground nesting ant species, because ground level territories are difficultly to defend (Hölldobler & Wilson 1990).

The species community in the area may be part of a characteristic ant mosaic for this forest type (see also Hölldobler & Wilson 1990, Davidson *et al.* 2007), but the identification of the dominant and submissive groups remains unclear.

The observations of trophobiotic interactions with *M. brunnea subcarinata* give little information about the host specificity of the observed species. Some of the cicadas were also found in trophobiotic interactions with other ant species, e.g. *Paratrechina* sp., which were located on neighbouring plants. Blüthgen *et al.* (2006) found clues for high host specificity of trophobiotic hemipterans regarding the host plant species but no tendency of ants to specialise on certain hemipterans or plants; ant species visiting the trophobionts were also subject to turnover over time. Hemipterans living on climbing bamboo seemed to be an important source of honeydew for *M. brunnea subcarinata* since more than half of the observed trophobioses were found on this plant, which has been considered as a keystone species for ants of the forest understorey (Mezger & Blüthgen 2007). Although trophobiotic interactions of ants and bugs are reported from only a few bug species in a small number of heteropteran families (Delabie 2001), associations between *Myrmicaria* and heteropterans have been frequently observed, e.g. in Africa *Myrmicaria opaciventris* is known to obtain honeydew from trophobiotic interactions with *Catenaultiella* bugs (Heteroptera; Plataspidae) (Gibernau & Dejean 2000; Dejean *et al.* 2000) and in Sabah a *Myrmicaria* species was observed at a trophobiosis with an unidentified plataspid bug (Mezger, pers. observation).

Taken together our current knowledge of the natural history of *M. brunnea subcarinata* remains sparse; future observations of this species should include more colonies and comprise the examination of the reproduction mode and the demography of the colony.

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